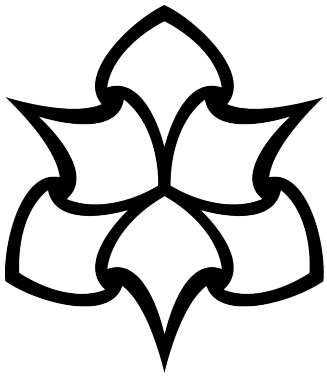

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RESEARCH ARTICLE

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Ecomorphology reveals Euler spiral of mammalian whiskers

Gary Dougill[1] | Eugene L. Starostin[2,3] | Alyx O. Milne[1] | Gert H. M. van der Heijden[3] | Victor G. A. Goss[2] | Robyn A. Grant[1]

[1]Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK

[2]School of Engineering, London South Bank University, London, UK

[3]Department of Civil, Environmental and Geomatic Engineering, University College London, London, UK

Correspondence
Robyn A. Grant, Department of Natural Sciences, Manchester Metropolitan University, Manchester, UK.
Email: robyn.grant@mmu.ac.uk

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Abstract

Whiskers are present in many species of mammals. They are specialised vibrotactile sensors that sit within strongly innervated follicles. Whisker size and shape will affect the mechanical signals that reach the follicle, and hence the information that reaches the brain. However, whisker size and shape have not been quantified across mammals before. Using a novel method for describing whisker curvature, this study quantifies whisker size and shape across 19 mammalian species. We find that gross two-dimensional whisker shape is relatively conserved across mammals. Indeed, whiskers are all curved, tapered rods that can be summarised by Euler spiral models of curvature and linear models of taper, which has implications for whisker growth and function. We also observe that aquatic and semi-aquatic mammals have relatively thicker, stiffer, and more highly tapered whiskers than arboreal and terrestrial species. In addition, smaller mammals tend to have relatively long, slender, flexible whiskers compared to larger species. Therefore, we propose that whisker morphology varies between larger aquatic species, and smaller scansorial species. These two whisker morphotypes are likely to induce quite different mechanical signals in the follicle, which has implications for follicle anatomy as well as whisker function.

KEYWORDS

curvature, mechanoreception, morphology, touch, vibrissae

1 | INTRODUCTION

Whiskers are present on the faces of almost all mammals (Ahl, 1986, 1987; Bauer, Reep, & Marshall, 2018; Ginter, DeWitt, Fish, & Marshall, 2012). They are specialised vibrotactile sensors that can guide behaviours such as navigation, locomotion, foraging, and social interactions (Grant & Arkley, 2015). Whiskers are grossly similar across mammals—being long, slender (Neimark, Andermann, Hopfield, & Moore, 2003), tapered (Ginter et al., 2012; Hires, Pammer, Svoboda, & Golomb, 2013; Williams & Kramer, 2010; Yanli, Wei, Yanchun, Jun, & Xiaoming, 1998) rods with an inherent curvature in one plane (Knutsen, Biess, & Ahissar, 2008; Towal, Quist, Gopal, Solomon, & Hartmann, 2011), suggesting a common (vibrotactile) function. Whisker specialists are species that can actively move their whiskers to sense, and include rodents, insectivores, and pinnipeds (Grant & Arkley, 2015; Muchlinski, Wible, Corfe, Sullivan, & Grant, 2020), suggesting that whiskers are especially useful for animals that live in dark, complex environments. Species that have the longest and most numerous whiskers also move their whiskers the most, and tend to be small, nocturnal, and arboreal (Grant, Breakell, & Prescott, 2018; Muchlinski, 2010; Muchlinski et al., 2020).

Whisker morphology can vary between species, for example, many phocids have undulating, beaded whiskers (Ginter et al., 2012; Ginter, Fish, & Marshall, 2010; Hanke et al., 2010; Rinehart, Shyam, & Zhang, 2017), and aquatic mammals are thought to have more innervated whiskers than terrestrial species (Dehnhardt & Mauck, 2008;

Mattson & Marshall, 2016; Mcgovern, Marshall, & Davis, 2015; Miersch et al., 2011; Rice, Mance, & Munger, 1986). Some aquatic species use their whiskers for both, touch and hydrodynamic sensing, such as California sea lions (*Zalophus californianus*; Gläser, Wieskotten, Otter, Dehnhardt, & Hanke, 2011; Milne & Grant, 2014) and Harbour seals (*Phoca vitulina*; Dehnhardt, Mauck, & Bleckmann, 1998; Grant, Wieskotten, Wengst, Prescott, & Dehnhardt, 2013), which may indicate functional differences between aquatic and terrestrial whiskers (Jones & Marshall, 2019; Sprowls & Marshall, 2019). Yet, while whisker shape and function are likely to differ between species, especially between aquatic and terrestrial species, the difficulty in comparing whisker shape quantitatively means that whisker morphology has not been explored across a wide range of mammalian species before. A recent study has found that whisker intrinsic curvature in rats (*Rattus norvegicus*) may be accurately described by linear functions so that the whiskers are well represented by intervals of the Euler spiral (Starostin, Grant, Dougill, van der Heijden, & Goss, 2020), which now offers a means for between-species comparisons.

Whiskers are differentiated from hair by their highly innervated, vascularised follicle (Ebara, Kumamoto, Matsuura, Mazurkiewicz, & Rice, 2002; Williams & Kramer, 2010). Mechanoreceptors within the follicle convert whisker force and moment information from the whisker into signals that the brain can encode (Ahissar & Knutsen, 2008; Diamond, Von Heimendahl, Knutsen, Kleinfeld, & Ahissar, 2008). Whisker size, including width and length, and the natural shape of each whisker, including taper and curvature, will affect the way in which the whisker deforms and vibrates, and hence, the signals within the follicle. This study quantifies the length, taper, and curvature of whiskers from 19 different mammalian species using the Euler spiral description of whisker curvature (Starostin et al., 2020) we go on to discuss how whisker morphology varies with animal size and substrate preference.

2 | MATERIAL AND METHODS

2.1 | Sample preparation

Thirty-four specimens of 19 species (Table 1, Supporting Information) were donated from collections at National Museums Scotland, or obtained from licensed suppliers. All work in this study was approved by the local ethics committee at Manchester Metropolitan University (Ethos ID: 364, 04/12/2008). Each species was coded for their general substrate preferences (Table 1), these groupings can often be difficult to define, as many of the species in our study are relatively flexible; these groupings were used for statistical analyses and then considered in more detail in the discussion.

Mystacial pads were dissected from specimens and fixed in 4% paraformaldehyde for a minimum of 24 hr for transport and storage. To improve image contrast during scanning, fixed pads were stained in a 1% Lugol's solution for 48 hr before individual whiskers were plucked from the pad. Whole, intact whiskers (including the papilla) were plucked from the mystacial pad. These were all macrovibrissae from the main rows and columns of the pads. Whisker layouts and numbers varied between species, but we attempted to pluck and collect all the mystacial macrovibrissae present in each individual specimen; this did not include the small rostral whiskers that were not in the grid-pattern, which were likely microvibrissae. Whiskers <5 mm long could not be consistently seen, removed, and imaged. Any whiskers with signs of damage were also rejected from the study. Where two whiskers emerged from the same follicle, the largest whisker was used.

2.2 | Individual whisker shapes

Six hundred and eighty-seven individual whiskers were scanned in two dimensions using an Epson V600 photo-scanner (Epson, Tokyo, Japan; resolution: 2–8 μm) to gather individual whisker shape parameters of curvature, length, and taper. Two-dimensional scanning methods were considered sufficient since whisker curvature has previously been observed to occur mostly in one plane (Knutsen et al., 2008; Towal et al., 2011) and all whiskers were able to lie flat on the scanning bed without deformation from the surface. Whisker outlines were extracted from images and processed by mapping to an Euler spiral. This was achieved by fitting the outline coordinates to edge model curves computed from an Euler spiral interval for each whisker centreline, a generalised procedure based on that described in Starostin et al. (2020). The papilla section was not included in the length or shape of the whisker. Curvature, κ, of whiskers was modelled as a linear function of their arclength, s, where A and B are constant coefficients, which differ for each whisker, so that the latter is approximated by an interval of an Euler spiral curve:

$$\kappa(s) = As + B \tag{1}$$

When dilated, all these intervals can be mapped onto the standard Euler spiral (Figure 1b), where the represented interval on the spiral, which is the arc length and position along the spiral, depends only on the whisker's shape. Using this method, whiskers from any species can be compared regardless of absolute size. Absolute whisker length (Table 1) was extracted during the curve fitting procedure and normalised against species body lengths taken from the literature to allow interspecies comparison.

Whisker taper was modelled as a linear function of whisker arc length and calculated by measuring the distance between the whisker centreline and the whisker edge (Supporting Information):

$$\text{half}-\text{width}(s) = \omega_0 + \omega_1 s \tag{2}$$

Coefficient ω_1 represents the taper gradient of the whisker; a negative value indicates a whisker that is thinner at the tip than the base. Coefficient ω_0 is the normalised whisker half-thickness at the base.

TABLE 1 Mean average values for all morphological parameters

Species	Common name	Family	Substrate	Curvature		Length		Taper		Body length (mm)
				A	*B*	(mm)	(%)	ω_0	ω_1	
Vulpes vulpes	Red fox	Canidae	Terrestrial	0.659	0.394	27.0	4.2	0.007	−0.005	644 (Rosenzweig, 1968)
Phodopus campbelli[a]	Campbell's dwarf hamster	Cricetidae	Terrestrial	0.686	0.414	17.4	18.3	0.004	−0.002	95 (Ross & Cameron, 1989)
Erethizon dorsatum	Common porcupine	Erethizontidae	Arboreal	0.058	0.886	28.7	4.9	0.004	−0.003	586 (Mclean, Carey, Kirk, & Bruce, 1993)
Suricata suricatta	Meerkat	Herpestidae	Terrestrial	0.037	0.546	19.3	7.2	0.005	−0.004	268 (van Staaden, 1994)
Hystrix africaeaustralis	Cape porcupine	Hystricidae	Terrestrial	1.241	0.433	81.0	10.8	0.005	−0.003	750 (Aarde, 1987)
Lepus timidus[a]	Mountain hare	Leporidae	Terrestrial	0.342	0.289	36.7	5.7	0.003	−0.002	644 (Schmidt & Jensen, 2003)
Micromys minutus	Harvest mouse	Muridae	Arboreal	−0.215	0.802	6.6	11.0	0.006	−0.005	60 (Koskela & Viro, 1976)
Mus musculus	House mouse	Muridae	Arboreal	0.397	0.131	11.4	13.3	0.005	−0.003	86 (Chakraborty, Park, & Tan, 2017)
Rattus norvegicus[a]	Brown rat	Muridae	Arboreal	0.349	0.348	26.0	10.2	0.004	−0.003	255 (Novelli et al., 2007)
Lutra lutra[a]	Eurasian otter	Mustelidae	Semi-aquatic	0.388	0.191	15.8	2.1	0.011	−0.008	750 (Garcia de Leaniz, Forman, Davies, & Thomson, 2006)
Mustela lutreola	European mink	Mustelidae	Semi-aquatic	0.866	0.227	19.9	4.9	0.007	−0.006	407 (Kiik, Maran, Nemvalts, & Sandre, 2017)
Mustela erminea	Stoat	Mustelidae	Terrestrial	0.470	0.459	20.1	9.2	0.004	−0.002	218 (Rosenzweig, 1968)
Mustela nivalis	Least weasel	Mustelidae	Terrestrial	1.478	−0.020	12.6	7.8	0.005	−0.004	161 (Rosenzweig, 1968)
Mustella putorius furo[a]	Ferret	Mustelidae	Terrestrial	1.526	−0.019	27.0	7.0	0.004	−0.002	386 (Blandford, 1987)
Halichoerus grypus	Grey seal	Phocidae	Aquatic	2.168	−0.363	48.4	2.0	0.013	−0.007	2,420 (Murie & Lavigne, 1992)
Phoca vitulina	Harbour seal	Phocidae	Aquatic	0.791	0.831	22.9	1.3	0.009	−0.008	1760 (Nørgaard & Larsen, 1991)
Crocidura russula	Greater white toothed shrew	Soricidae	Terrestrial	0.317	0.300	8.7	12.3	0.005	−0.003	71 (Sánchez-Chardi & Nadal, 2007)
Sorex araneus	Common shrew	Soricidae	Terrestrial	1.275	0.130	10.6	17.6	0.006	−0.004	60 (Frafjord, 2008)
Sorex minutus	Pygmy shrew	Soricidae	Terrestrial	−0.048	0.723	10.0	19.7	0.003	−0.002	51 (Grainger & Fairley, 2009)

Note: Overall, whisker measures included normalised whisker length, two curvature coefficients (A and B), and two taper coefficients (ω_0 and ω_1). Species body lengths are taken from the literature.

[a]Obtained from licensed suppliers and all others donated from the collections at National Museums Scotland.

2.3 | Statistics

Multivariate analysis of variances (ANOVAs) were conducted on the full 687-whisker data set; environmental substrate was used as the between-factor with morphological parameters *A*, *B*, Normalised Length, ω_0, and ω_1 as dependent variables. A Bonferroni corrected *p* value ($p < .01$) was used to indicate significance and Bonferroni post-hoc test used for between-substrate effects. Partial eta squared was used as a measure of effect size with 0.06 suggesting a medium effect and 0.14 a large effect (Cohen, 2013). Pairwise Spearman's rank correlations were also conducted on mean average species values (whisker *A*, *B*, Normalised Length, ω_0, ω_1, body length, Table 1).

To reduce dimensionality of data, principal component analysis (PCA) was conducted on the entire data set of 687 whiskers using the five measures: *A*, *B*, Normalised Length, ω_0, and ω_1. The two principal components, accounting for the majority of variation were then further analysed. Multivariate ANOVA was performed on principal component scores using environmental substrate as the between-factor with PC1 and PC2 as dependent variables ($p < .05$ significance level), partial eta squared was used for effect size.

3 | RESULTS

Whisker centreline curvature was approximated by an Euler spiral in all species (fitting residual *SD* [RSD] < 1% of whisker length in 98% of whiskers; Figure 1b). Coefficient of curvature *B* did not vary significantly between species' substrate preferences, although Coefficient

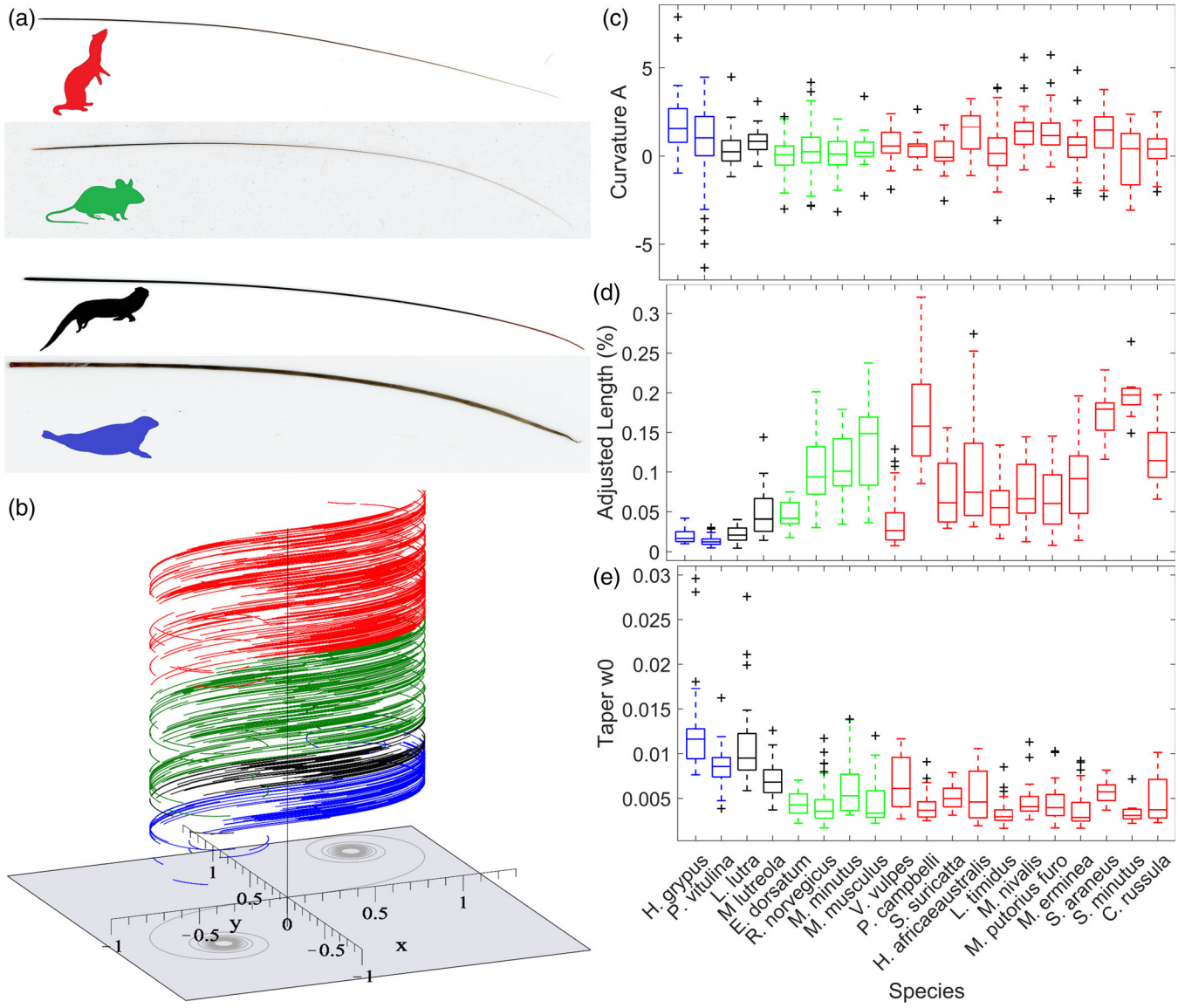

FIGURE 1 Comparative whisker shapes in mammals (a) Example scanned whiskers; Ferret (Length [L] = 34.5 mm, Base Width [BW] = 0.23 mm), Rat (L = 19.6 mm, BW = 0.18 mm), Otter (L = 25.2 mm, BW = 0.3 mm) and Grey Seal (L = 68.9 mm, BW = 1.41 mm). (b) An Euler plot of all 687 whiskers normalised for length. Individual whiskers are stacked on one another (in the y-axis) and their position on the spiral indicates their shape. Whisker curvature (c), normalised whisker length (d) and whisker taper (e) of each species. Boxes are coloured according to typical substrate: terrestrial (red), arboreal (green), aquatic (blue), and semi-aquatic (black). Box-plot whiskers extend to the most extreme data points that are not outliers, with outliers defined as values greater than three *SD*s from the mean

of curvature *A* did (Table 2), specifically it was observed that semi-aquatic mammals had lower values than aquatic mammals (Figure 1c) and arboreal mammals had higher values than terrestrial species, and lower values than aquatic species.

A linear taper function was a good fit to whisker outlines in all species (RSD < 2% of whisker length) and varied significantly with species' substrate preferences (Table 2, Figure 1e). Overall, aquatic and semi-aquatic species had significantly larger taper coefficients than terrestrial and arboreal mammals (Figure 1e). Normalised whisker lengths also varied significantly between species, with aquatic and semi-aquatic animals having smaller normalised whisker lengths than terrestrial and arboreal mammals. Species body length was also correlated with normalised whisker length, where smaller species had longer normalised whisker lengths (Spearman's rank [SR]: r^2 = –.76, p < .001). Patterns in substrate preferences were confirmed in mustelid species to test whether patterns across mammal species were consistent within a single family. Results confirmed that aquatic and semi-aquatic species had significantly different normalised whisker lengths and taper to arboreal and terrestrial species; with smaller but still significant variation in curvature coefficient A observed between semi-aquatic and terrestrial mustelids. (Table 2).

Principal component (PC) 1 and 2 represented 47.9 and 35.6% of variation in whisker parameters for the full data set. PC1 was most correlated with normalised length (r^2 = .57) and taper (ω_0: r^2 = .87; ω_1:

TABLE 2 Results of multivariate ANOVA

		MANOVA		
All species		***F***	***p***	η_p^2
Original data	*A*	10.610	<.001	0.047
	B	2.656	.048	0.012
	Length	99.967	<.001	0.318
	ω_0	142.575	<.001	0.399
	ω_1	147.224	<.001	0.407
		F	***p***	η_p^2
PCA	PC1 (47.9%)	185.848	<.001	0.464
	PC2 (35.6%)	3.434	.017	0.016
Mustelidae		***F***	***p***	η_p^2
Original data	*A*	8.568	.004	0.051
	B	0.483	.488	0.003
	Length	70.841	<.001	0.371
	ω_0	77.595	<.001	0.393
	ω_1	79.659	<.001	0.399
		F	***p***	η_p^2
PCA	PC1 (52.7%)	91.902	<.001	0.434
	PC2 (34.4%)	9.289	.003	0.072

Note: Statistical effects of environmental substrate on whisker morphological parameters and principal component scores. A Bonferroni corrected significance value of .01 is used. Medium and large effects are defined as partial eta squared values of over 0.06 and 0.14, respectively.
Abbreviations: MANOVA, multivariate analysis of variance; PCA, principal component analysis.

r^2 = .86), whereas PC2 was most correlated with curvature (*A*: r^2 = .85; *B*: r^2 = .85), suggesting that whisker length and taper captures the most variation in our data. When plotted against one another they formed an amorphous cluster centred at the origin of the morphospace, with most species and families spread throughout. However, semi-aquatic and aquatic species tended to be on the right-hand side of the plot with larger values of PC1 (Figure 2a; Table 2). Indeed, species' substrate preferences had large, significant effects on PC1 (Figure 2b) and small, significant effects on PC2 (Figure 2c). Post-hoc tests confirmed that PC1 was larger in aquatic and semi-aquatic species, than in terrestrial and arboreal species (Figure 2b). These findings were also confirmed in mustelid species, the only family of those investigated where different substrates (terrestrial and semiaquatic) are observed. When principal component analysis was conducted on mustelid species alone, PC1 and 2 explained 52.7 and 34.4% of variation in whisker parameters, and substrate preference had large, significant effects on PC1 (Table 2) and medium, significant effects on PC2.

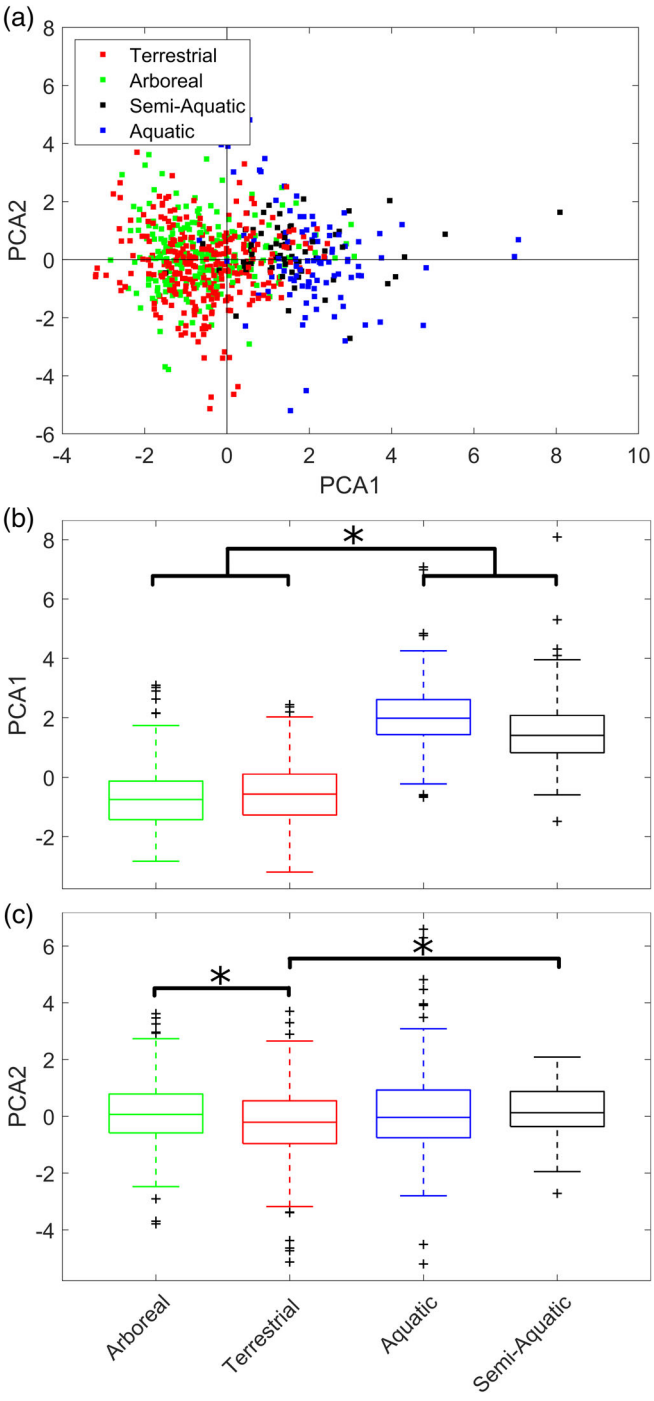

FIGURE 2 Principal component analysis (PCA) of whisker shape. (a) PC1 plotted against PC2 for all species. (b) PC1 values according to typical substrate. (c) PC2 values according to typical substrate. Black asterisks indicate significant differences. Value colours indicate typical substrate: terrestrial (red), arboreal (green), aquatic (blue) and semi-aquatic (black)

4 | DISCUSSION

Using an Euler spiral, we are now able to quantify and compare the curvature of whiskers from a wide range of mammalian species, regardless of their absolute size. That whisker curvature obeys a simple linear relationship with length has previously been observed only in rats (Starostin et al., 2020). We observe it here in many different species. Therefore, the Euler spiral could be found across mammalian whiskers and may indicate that a common ancestor would have similarly curved whiskers.

4.1 | Whisker shape approximations

Accurately measuring and modelling whisker curvature is of significant importance in whisker mechanics. The intrinsic curvature of whiskers likely improves object localisation (Huet, Rudnicki, & Hartmann, 2017) and forms part of the kinematic basis for texture discrimination (Zuo & Diamond, 2019). Many vibrissae have curvature that is noticeable to the eye, either straightening or curling along their length. Whiskers can also include an inflection point, where they curve first one way and then the other. The Euler spiral model can approximate all of these observed shapes. None of the whiskers that we measured included a curvature with more than one inflection (e.g., a sine wave). These aforementioned observations suggest that a constant, or circular, curvature model is not able to capture all aspects of observed whisker shape, whereas a model with a high-degree polynomial curvature is unnecessarily complicated (Summarell, Ingole, Fish, & Marshall, 2015). Other studies have approximated whiskers as quadratic curves (Quist & Hartmann, 2012; Towal et al., 2011), which cannot replicate inflections in curvature, or otherwise used cubic splines to capture whisker shape (Bagdasarian et al., 2013; Belli, Bresee, Graff, & Hartmann, 2018), but these are challenging to compare with one another. It is also possible to compare whisker outlines fitted with Elliptic Fourier harmonic coefficients (Ginter et al., 2012) or Bezier curves (Campagner, Evans, Loft, & Petersen, 2018; Hewitt et al., 2018; Petersen, Colins, Evans, Campagner, & Loft, 2020); although these are good visual representations of whisker shape, they do not provide a clear and succinct equation, which is useful for developing mechanical models. Therefore, as previously observed in rats (Starostin et al., 2020), we propose that a two parameter, linear curvature function (Equation 1) provides a good approximation for whisker curvature. Moreover, it fits measured whisker shapes with a high degree of accuracy in all species tested (fitted curves have RSD < 0.8% of whisker length in 98% of all whiskers). This simple relationship between curvature and length may be explained by common growth mechanisms underlying mammalian whisker development, akin to the simple growth rules of spiral sea shells (Thompson, 1942). There have only been a few studies on whisker growth. For some species of phocids it has been described as irregular, with periods of pause (Greaves, Hammill, Eddington, Pettipas, & Schreer, 2004; Hirons, Schell, & St. Aubin, 2001). However, a linear fit has been reported for mice and some species of Pinnniped (Greaves et al., 2004; Hirons et al., 2001; Ibrahim & Wright, 1975). While species-specific variation may occur in whisker growth, a largely linear relationship may explain why little variation is seen in the intrinsic curvature of whiskers across species.

A linear function is also able to capture the overall trend of whisker taper from thick base to thinner tip. However, it is worth bearing in mind that whilst a linear function of taper is able to fit whisker outlines with low residuals (RSD < 2% of whisker length), many whiskers, such as those of harbour seals, are observed to have undulating surfaces, the details of which are not captured by linear functions. In spite of this, those whiskers that have undulating surfaces still progressively reduce in thickness from base to tip, with "beads" or undulations close to the tip being smaller in diameter than those at the base (Ginter et al., 2010, 2012; Hanke et al., 2010; Summarell et al., 2015). Whisker taper has been identified as a key morphological property of whiskers that improves both tactile and distance discrimination (Hires et al., 2013, 2016; Williams & Kramer, 2010) as well as 3D-object localisation (Huet et al., 2017). However, while taper and curvature are suggested to improve aspects of tactile sensing, it is unclear how these two parameters might impact other aspects of whisker sensing, such as hydrodynamic signal detection.

4.2 | Aquatic and terrestrial whiskers

Whisker taper and normalised length, approximated by PC1, described the most variation in whisker shape in our data. In particular, taper and length significantly differed between our species, such that aquatic and semi-aquatic whiskers have shorter (normalised length) whiskers that are thicker at the base (larger taper coefficient ω_0) and more extremely tapered (larger taper coefficient ω_1). Previously, it has been suggested that whisker specialists with many, long whiskers are found on small, nocturnal, climbing animals (Ahl, 1987; Muchlinski, 2010; Muchlinski et al., 2020; Pocock, 1914). We confirm this with the correlations found in our data, that smaller mammals have relatively longer and more slender whiskers than larger mammals. This can be observed in *Sorex araneus*, *Sorex minutus*, *Crocidura russula*, *Micromys minutus*, and *Mus musculus* (Table 1), all of which are small rodents or insectivores, with the capability of climbing, although not strictly identified as arboreal in our data.

Many aquatic mammals are also considered whisker specialists (Bauer et al., 2018; Grant & Arkley, 2015), and we suggest that they have a different whisker morphology, better able to cope with sensing in an aquatic environment. Specifically, that they have stiffer whiskers that are shorter and wider at the base with high taper gradients. It has previously been suggested that whisker taper allows for a fine, sensitive tip whilst the increased basal diameter maintains the overall rigidity of the whisker, allowing the follicle musculature to position the tip accurately (Summarell et al., 2015; Williams & Kramer, 2010). In aquatic environments, where fluid flow is liable to subject whiskers to larger forces, increased basal diameters may help to maintain intrinsic whisker shape and control of tip position, whilst the relatively shorter length of aquatic whiskers reduces drag (Hanke, Wieskotten, Marshall, & Dehnhardt, 2013). Conversely, slender and more flexible whiskers found on terrestrial mammals will bend and deflect more easily around environmental objects when exploring in tight, enclosed spaces.

Adaptation to the aquatic environment is likely to be a key driver in whisker morphology, especially in pinnipeds. Pinniped whiskers are morphologically diverse compared to other species. Whereas most mammalian whiskers have circular cross sections, those of phocids and otariids are better described by an ellipse (Ginter et al., 2010, 2012). This means that pinniped whiskers are stiffer in the direction where the whiskers are thicker (along the major axis) (Summarell et al., 2015). However, the difference in diameter between the major

and minor axes can be quite variable; Grey seals (*Halichoerus grypus*) have more elliptical whiskers in cross-section, and Weddell seals (*Leptonychotes weddellii*) have more circular whiskers (Summarell et al., 2015). The most studied whisker adaptation in pinnipeds is the presence of undulations along the shaft, which are observable in most phocids (Ginter et al., 2010, 2012; Gläser et al., 2011; Hanke et al., 2010; Krüger, Hanke, Miersch, & Dehnhardt, 2018; Niesterok, Dehnhardt, & Hanke, 2017; Summarell et al., 2015) (Figure 1a). These undulations are believed to reduce signal to noise ratios in flowing water (Hanke et al., 2010; Kottapalli, Asadnia, Miao, & Triantafyllou, 2015). Summarell et al. (2015) found that smooth whiskers were stiffer than undulating whiskers. Since phocids, with undulating whiskers, tend to be better at hydrodynamic tasks (Gläser et al., 2011; Hanke et al., 2013; Krüger et al., 2018; Niesterok et al., 2017), the authors suggest that having some flexibility of the whiskers might be useful for hydrodynamic sensing in phocids, while stiffer whiskers might be better for touch sensing in otariids. While we suggest here that aquatic mammal whiskers are stiffer than those of terrestrial mammals, for otariids and phocids, a more complex three-dimensional approach may be needed in order to fully compare whisker stiffness between these species, especially to better understand the functional significance of whisker stiffness.

The quick and easy scanning and analysis methods that we propose here are able to accurately capture gross measures of whisker curvature and taper, enabling lots of data to be collected for comparative analyses. The linear taper and curvature models described here provide a basis for comparison that can serve as benchmarks. These methods are especially suitable for species that are likely to have circular whisker cross-sectional shapes, such as in terrestrial mammals; however, they cannot capture all the observed variation in morphology that occurs in otariids and phocids. Incorporating two-dimensional measures of taper and curvature into bio-mechanical models is also a challenge. The interplay between morphology, mechanics, and vibrotactile sensing is complex and not well-understood. Damping will occur within the follicle and will depend on the follicle anatomy, blood supply, and surrounding muscles, which all might be under active, or passive, control (Hartmann, Johnson, Towal, & Assad, 2003; Hyvärinen, 1989; Mitchinson et al., 2004). The arrangement of mechanoreceptors within follicles will also vary from species to species (Ebara et al., 2002; Hyvärinen, 1989; Jones & Marshall, 2019; Marshall, Amin, Kovacs, & Lydersen, 2006; Sprowls & Marshall, 2019), so exactly how and where whisker deflections and vibrations are detected will vary between species. It is evident that there is much to learn about whiskers; further studies could usefully explore relationships between morphological variation and evolutionary adaptations, in particular with respect to the "whisker specialists," including aquatic and scansorial mammals.

5 | CONCLUSIONS

Gross two-dimensional whisker shape is relatively conserved across mammals and can be summarised by Euler spiral models of curvature and linear models of taper. We find that small mammals tend to have relatively long, slender, and flexible whiskers, while aquatic mammals have relatively thicker, stiffer, and shorter whiskers. Both of these groups are often considered whisker specialists. While whisker specialists may commonly use their whiskers for navigation and foraging in their dark, complex environments, the mechanical implications of these two whisker morphotypes are likely to affect mechanical signals in the follicle, as well as whisker function.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Eugene Starostin: Formal analysis; investigation; methodology; software; writing-review and editing. **Alyx Milne:** Formal analysis; resources; writing-review and editing. **Gert van der Heijden:** Formal analysis; investigation; methodology; software; writing-review and editing. **Geoff Goss:** Funding acquisition; investigation; methodology; project administration; writing-review and editing. **Robyn Grant:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; resources; writing-original draft; writing-review and editing.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

ORCID

Gary Dougill https://orcid.org/0000-0002-8885-6166

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SUPPORTING INFORMATION

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